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Response of the larger protozooplankton to an iron-induced phytoplankton bloom in the Polar Frontal Zone of the Southern Ocean (EisenEx)

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Abstract

The responses of larger (>50 μm in diameter) protozooplankton groups to a phytoplankton bloom induced by in situ iron fertilization (EisenEx) in the Polar Frontal Zone (PFZ) of the Southern Ocean in austral spring are presented. During the 21 days of the experiment, samples were collected from seven discrete depths in the upper 150 m inside and outside the fertilized patch for the enumeration of acantharia, foraminifera, radiolaria, heliozoa, tintinnid ciliates and aplastidic thecate dinoflagellates. Inside the patch, acantharian numbers increased twofold, but only negligibly in surrounding waters. This finding is of major interest, since acantharia are suggested to be involved in the formation of barite ($BaSO_4$), a palaeoindicator of both ancient and modern high-productivity regimes. Foraminifera increased significantly in abundance inside and outside the fertilized patch. However, the marked increase of juveniles after a full-moon event suggests a lunar periodicity in the reproduction cycle of some foraminiferan species rather than a reproductive response to enhanced food availability. In contrast, adult radiolaria showed no clear trend during the experiment, but juveniles increased threefold, indicating elevated reproduction. Aplastidic thecate dinoflagellates almost doubled in numbers and biomass but also increased outside the patch. Tintinnid numbers decreased twofold, although biomass remained constant because of a shift in the size spectrum. Empty tintinnid loricae, however, increased by a factor of two, indicating that grazing pressure on this group mainly by copepods, intensified during EisenEx. The results show that iron-fertilization experiments can shed light on the biology and the role of these larger protists in pelagic ecosystem, which will improve their use as proxies in paleoceanography.

Keywords: Iron fertilization; Protozooplankton; Acantharia; Barite; Polar Front; Southern Ocean

1. Introduction

Despite the extensive use of their mineral skeletons as proxies for palaeoceanographic reconstructions, studies of the diversity and the function of larger protozooplankton (>50 μm) in pelagic food webs in the Southern Ocean are fairly recent (Gowing and Garrison, 1991; Nöthig and Gowing, 1991; Gowing and Garrison, 1992; Gowing et al., 2001; Klaas, 2001). This size class of the protistan plankton tends to be neglected in standard pelagic studies because larger protozoa are not adequately

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represented in water samples examined for phytoplankton nor in net samples for zooplankton. Yet their standing stocks in terms of biomass, albeit generally lower than that of smaller protozooplankton ($<50\,\mu m$), can attain the same range as that of metazooplankton: $>0.5\,g\,C\,m^{-2}$. Hence, larger protozooplankton ($>50\,\mu m$) can be expected to play a significant role in pelagic food webs (Alder and Boltovskoy, 1993).

The phylogenetically heterogeneous taxonomic groups making up this size class differ widely in their ecology and their impact on biogeochemical cycles. Large ciliates and dinoflagellates are abundant herbivores, and the carbonate and siliceous skeletons of foraminifera and radiolaria, respectively, contribute significantly to the underlying sediments (reviewed by Caron and Swanberg, 1990; Garrison and Gowing, 1993). Due to their barium (Ba)-enriched celestite ($Ba/Sr,SO_4$) skeletons, acantharia play a unique role in the Ba and strontium (Sr) cycles (Bernstein et al., 1987, 1992, 1998), and it has thus been suggested that these organisms influence Ba deposition in the sediments. The degree of barite ($BaSO_4$) deposition in the sediments is used as a proxy for productivity of the overlying water, although the mechanisms leading to its formation are under debate (Dehairs et al., 1991, 1992, 1997; Dymond et al., 1992; Francois et al., 1995; Dymond and Collier, 1996; Esser and Volpe, 2002; Bernstein and Byrne 2004).

Field observations of foraminiferan and radiolarian abundances, vertical distribution patterns and food web interactions in the Southern Ocean have been carried out in the Weddell Gyre and Weddell–Scotia Confluence (WSC) during austral autumn (Abelmann and Gowing, 1996, 1997) and austral winter (Gowing and Garrison, 1991; Nöthig and Gowing, 1991; Gowing and Garrison, 1992). Results from these studies indicate high variability of abundance, biomass and assemblage composition depending mainly on season and region. Klaas (2001) followed the temporal development of abundances, vertical zonation and community composition of all important taxa during the austral spring along a meridional transect across the Polar Frontal Zone (PFZ) of the Southern Ocean. Her results suggest highest abundances in the Polar Front (PFr) concurrent with phytoplankton blooms and that spring distribution patterns of most groups follow productivity in the water column.

Iron-fertilization experiments provide an ideal context to study the responses of the different protozoan groups to an increase in food supply under in situ conditions. In this study, we followed the responses of larger ($>50\,\mu m$) sarcodinid protozoa (i.e., acantharia, foraminifera, radiolaria and heliozoa), tintinnid ciliates and aplastidic thecate dinoflagellates to a phytoplankton bloom induced during an iron-fertilization experiment in the PFZ of the Southern Ocean (EisenEx). Our aims were to investigate the role of these organisms as a trophic link between smaller protozooplankton and larger metazooplankton (Gowing, 1989) and to study a size fraction and group of taxa of which some are important for paleoceanographic studies (Boltovskoy and Alder, 1992; Boltovskoy et al., 1996; Abelmann and Gowing, 1996, 1997).

2. Material and methods

The mesoscale in situ iron-fertilization experiment EisenEx was conducted in the Atlantic Sector of the Southern Ocean (47°S, 21°E) in austral spring (8–29 November 2000) during the cruise ANT XVIII/2 of the R/V *Polarstern*. A cyclonic eddy (approximately 120 km wide) shed by the Antarctic PFr was chosen as the "container" for the experiment and its center marked with a drifting buoy. An area of about $40\,km^2$ around the buoy was fertilized with four tons of iron sulfate added as acidified solution ($Fe(II)SO_4$) on three occasions at 8-day intervals (Cisewski et al., 2005). Sulfur hexafluoride (SF_6) was added as an inert tracer at the first iron infusion in order to mark the iron fertilized "patch" (Watson et al., 2001). Inside and outside stations were chosen according to SF_6 concentrations measured along surface surveys. The "in-stations" were situated at the highest observed SF_6 concentrations, whereas "out-stations" were located in adjacent waters with background SF_6 concentrations. The day of the first fertilization (day 0) was referred to as the reference station. A detailed description of the temporal evolution of water column properties during Eisen-Ex is given in the discussion section below.

2.1. Abundance

For quantitative assessment of acantharia, radiolaria, foraminifera, heliozoa, tintinnid ciliates and aplastidic thecate dinoflagellates $>50\,\mu m$, water samples were taken from seven discrete depths (10, 20, 40, 60, 80, 100 and 150 m) at 11 in- and 5 out-patch stations with 12 L Niskin bottles mounted on